Rete Mirabile Ophthalmicum and Intercarotid Anastomosis in Procellariiformes Taken off the North Carolina Coast

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ABSTRACT.— Dissections of arterial circulation patterns were made in eleven species of procellariiform birds taken off the coast of North Carolina. All species possessed well-developed rete mirabile ophthalmicums (RMO) and intercarotid anastomoses, both playing a role in selectively shunting blood flow and counter-current heat exchange to facilitate thermoregulation and maintaining brain temperatures lower than body temperatures during heat stress. There was no correlation between relative size of the RMO and nesting latitude, but RMO size was relatively greater in the smaller members of the order.

INTRODUCTION

Kilgore et al. (1979) and Bernstein et al. (1979a, 1979b) showed that the presence of a rete mirabile ophthalmicum (RMO) was associated with a reduction in brain temperature in heat stressed birds. The rete facilitates counter-current heat exchange between the arterial blood supply to the brain and the venous blood draining the evaporative surfaces of the mouth and the cornea. RMO's have been reported in a number of species (Richards and Sykes 1967; Lucas 1970; Kilgore et al. 1976; Crowe and Crowe 1979; Pettit et al. 1981). Pettit et al. (1981) examined the anatomy of the RMO of Hawaiian seabirds that may encounter stressful thermal environments at their tropical nesting sites. An additional site for possible counter-current heat exchange lies in the cavernous sinus that houses the carotid vein and the intercarotid anastomosis (Baumel and Gerchman 1968). These authors described three major types of intercarotid anastomoses in birds.

My study was undertaken to determine if the RMO and the type of intercarotid anastomosis in procellariiform birds breeding near the poles, in the temperate zones, and in the tropics differed, perhaps in response to thermal stresses encountered at the nesting colony. One might predict that tropical, open, ground-nesting species are exposed to greater thermal stress and therefore would have relatively larger retes.

METHODS

Most specimens were collected 30 to 60 km off the North Carolina

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coast, but a few specimens of the Northern Fulmar, *Fulmarus glacialis*, and the Sooty Shearwater, *Puffinus griseus*, were found dead on North Carolina beaches. The lone Antarctic Petrel, *Thalassoica antarctica*, was obtained from D. G. Ainley via D. W. Johnston in trade. All specimens on which this note is based are deposited in the collection of the North Carolina State Museum of Natural History. Dissections under a binocular microscope were in most cases performed on pickled specimens, using the methodology of Pettit et al. (1981).

RESULTS

Two of the three types of intercarotid anastomoses were found in the eleven procellariiform species examined in this study (Table 1). There was no correlation of anastomosis type with latitude (as an index of potential thermoregulatory stress).

In all cases the RMO was found in the temporal region of the head, between the orbital ridge and the otic process of the quadrate. The RMO is derived from the external ophthalmic branch of the internal carotid artery and from branches of the facial, maxillary and mandibular veins. To crudely assess the relative size of the rete in 11 species of Procellariiformes ranging in weight from 34 to 774 grams, I measured the surface area of the RMO using a transparent grid. This measure does not take into account the relative thickness or, more importantly, the actual area of contact of the arterial and venous components of the rete. However, it does give a first approximation of the relative size of the rete. Surface area/body weight ratios exhibited a slight but insignificant ($P>0.05$) increase with latitude (Table 2), while an inverse correlation ($P<0.05$) of body weight and RMO surface area/weight ratio was evident. Thus, the smaller procellariiforms have relatively larger RMO's.

DISCUSSION

A well-developed intercarotid anastomosis unites the two carotids caudal to the hypophysis in most birds examined by Baumel and Gerchman (1968). They found that injection of the cervical portion of one carotid resulted in bilateral filling of both the intra- and extracranial arteries via this anastomosis. The avian intercarotid anastomosis may effectively substitute for the mammalian circle of Willis in maintaining brain-to-body temperature differences (Baumel and Gerchman 1968; Kilgore et al. 1976; Pettit et al. 1981).

As Kilgore et al. (1976) pointed out, the effectiveness of the RMO heat exchange depends on the arterial-venous temperature differential, on rete blood flow and velocity, and the area and closeness of arterial-venous contacts within the rete.

Several species, including Sooty and Greater Shearwaters, and Wilson's Storm-Petrel, *Oceanites oceanicus*, are transequatorial migrants

Table 1. Pattern of intercarotid anastomosis in 46 specimens of 11 species of Procellariiformes. N = number examined.

Species	N	Pattern of anastomosis[1]			Latitude of breeding range[2]
		X	X-H	H	
Fulmarus glacialis	2	2			50-85° N
Thalassoica antarctica	1	1			72-76° S
Pterodroma hasitata	4	4			14-20° N
Calonectris diomedea	13	13			14-40° N
Puffinus gravis	4	4			36-40° S
Puffinus griseus	3	3			52-56° S
Puffinus puffinus	2	2			28-65° N
Puffinus lherminieri	7	7			10-33° N
Oceanites oceanicus	8	4	3	1	51-75° S
Oceanodroma leucorhoa	1	1			42-64° N
Oceanodroma castro	1	1			30-40° N

[1]X-type is defined as having cerebral carotids anastomosing side-to-side, H-type has a pronounced transverse anastomosis joining the two carotids, and X-H type is intermediate with a short transverse anastomosis (after Baumel and Gerchman 1968).

[2]from Palmer (1962) or Watson (1975).

that may be exposed to thermal stress while flying across the doldrums (equatorial zone with little wind). Their retes are not appreciably larger than those of north or south temperate zones or Antarctic species. Birds collected while they were flying at sea off North Carolina did not exhibit elevated body temperatures (Platania et al., in press). The RMO of the Black-capped Petrel, *Pterodroma hasitata*, a tropical species, is not different from that of other species of higher latitudes. The bird is not subjected to heat stress at its nesting grounds because it is a winter (Northern Hemisphere) breeder, and because at high elevations it excavates burrows. Altitude, and the extent of the use of burrows for nesting, further cloud simple correlations of RMO ratios with latitude. In general, the smaller birds nest exclusively in burrows or crevices while the larger shearwaters and fulmars are open ground or cliff nesters. In addition, most ground-level activity of burrowing species occurs at night, further reducing heat stress.

As arterial blood may reach the brain via several routes (Richards and Sykes 1967; Richards 1970; Crowe and Crowe 1979), involving both direct and indirect (via extensive anastomoses) flow, the potential exists for selectively regulating flow under varying conditions. Flow of arterial blood may be shunted through the RMO to the brain via anterior anastomoses with intracranial branches of the internal carotid. This could

Table 2. Surface area of rete and body weight ratios of 11 species of Atlantic Procellariiformes. Data presented as mean ± 1 standard deviation (sample size).

Species	Rete surface area (mm²)	Weight of birds (g)	Surface area/ weight (mm²/g)	Average breeding latitude
Northern Fulmar *Fulmarus glacialis*	35.10±0.92(2)	692.3±78.5(20)[a]	0.05	67° N
Antarctic Petrel *Thalassoica antarctica*	28.60(1)	639[b]	0.04	74° S
Black-capped Petrel *Pterodroma hasitata*	32.11±6.21(5)	431.1±47.1(5)	0.07±0.01(5)	17° N
Cory's Shearwater *Calonectris diomedea*	31.45±3.18(13)	568.8±80.6(12)	0.06±0.01(12)	27° N
Greater Shearwater *Puffinus gravis*	36.08±1.50(4)	626.6±29.9(3)	0.06±0.01(3)	38° S
Sooty Shearwater *Puffinus griseus*	36.18±1.35(3)	774.0(1)[a]	0.04	54° S
Manx Shearwater *Puffinus puffinus*	26.00±1.84(2)	359.2±34.0(2)	0.07±0.01(2)	47° N
Audubon's Shearwater *Puffinus lherminieri*	14.67±1.98(7)	179.8± 4.4(6)	0.08±0.01(6)	22° N
Wilson's Storm-Petrel *Oceanites oceanicus*	3.49±0.77(8)	34.3± 2.9(6)	0.10±0.02(6)	63° S
Leach's Storm-Petrel *Oceanodroma leucorhoa*	3.90(1)	40.8(1)	0.10(1)	53° N
Band-rumped Storm-Petrel *Oceanodroma castro*	4.55(1)	48.4(1)	0.09(1)	35° N

[a]from Platania et al. (in press)
[b]mean of values in Brown et al. 1982

serve to maintain brain temperatures lower than core body temperatures during heat stress (Kilgore et al. 1979; Bernstein et al. 1979a, b). During cold stress the arterial blood flowing to the anterior surface of the head is cooled by returning venous blood in the RMO (Frost et al. 1975). Undue loss of body heat is prevented in the RMO by counter-current heat exchange. In this example, the anastomoses with the intracranial arteries are not open; blood flow to the brain is achieved directly via the internal carotid. Therefore, the lack of correlation between size of RMO and latitude (as an indicator of temperature stress) may indicate that the RMO functions during both cold and heat stress. The relatively larger RMO in smaller birds is probably related to their relatively larger surface/volume ratios, and the relatively greater stress they encounter as environmental temperatures fluctuate.

In summary, all 11 species of procellariiform birds examined possessed a rete mirabile ophthalmicum. There was no correlation between relative size of RMO and nesting latitude, but RMO size was relatively greater in the smaller members of the order.

ACKNOWLEDGMENTS.— Most of the specimens examined were collected by David S. Lee and colleagues at the N.C. State Museum of Natural History under a contract (#92375-1130-621-16) from the Slidell, Louisiana, laboratory of the U.S. Fish and Wildlife Service. This is contribution number 1985-4 of the North Carolina Biological Survey.

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Accepted 19 July 1984